THE EFFECT OF RATE, FREQUENCY, AND FORM OF MIGRATION ON HOST PARASITE POPULATION DYNAMICS

By

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Abstract

What is the effect of migration on host-parasite population dynamics? Animals live in a landscape where they move between patches. They are also locked in host-parasite conflicts. Host-parasite interactions are modeled with consumer resource functions. I constructed models using two different consumer resource functions (the Lotka Volterra system and the Saturating Type II system). The first model was a conservative system. The second was dissipative and more biologically realistic. I examined the effect of rate of migration, time between migration events, and form of migration.

I found that the time between migration events had the largest effect on the synchronization in host-parasites population dynamics between the patches. Decreased time between migration events increased the fraction of simulation to completely synchronize and decreased the time it took to do so. In the first model, I observed simulations with a low rate of migration took a long time to synchronization and with a high rate of migration took a short time to synchronize. There was a phase transition between these two amounts of time it took to synchronize. In the second model, simulations done at low rates of migration did not synchronize while with increased migration rates the fraction of simulations to synchronize increased. I found in some simulations of parasite only migration that the patches synchronized faster. My results imply that parasite only migration to islands could have a greater impact on the extinction risk on islands further from the mainland than other forms of migration.

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Chapter 1: Introduction and Background

Dispersal and migration are extremely common and important in nature. At the population level dispersal is often called migration; this is not to be confused with migration in the ecological sense where individuals regularly move from one environment to another (Matthysen, 2012). Ecological migration is a subset of the population level migration. I will focus on the latter. Migration serves three major functions (Matthysen, 2012). First, an organism moving from its natal habitat reduces its likelihood of interacting with kin thereby avoiding competition with kin and inbreeding (Matthysen, 2012). Second, dispersal increases the variance in the expected fitness of offspring from the same parents (Matthysen, 2012). Spreading offspring out acts as a hedge-betting strategy because the offspring end up in a wide range of habitats, increasing the likelihood that at least some offspring will reproduce (Matthysen, 2012). Third, dispersal allows for escape of unfavorable local conditions such as overcrowding or a high concentration of predators by an individual (Benton & Bowler, 2012a).

This being said, migration is costly for the individual. An organisms' genes are suited to the natal environment where its parents were successful and there is no guarantee those genes will be well adapted anywhere else (Drown, et al., 2013). The action of migrating costs energy (Matthysen, 2012). Organisms often must grow wings or develop strong limbs to propel them when migrating (Ronce & Clobert, 2012). Migration is dangerous for the individual (Matthysen, 2012). Being in unfamiliar habitat increases the risk of predation, risk of getting off course, and decreases the likelihood of finding food and shelter (Matthysen, 2012).

Migration happens in a landscape. From an organism's perspective, this landscape is broken up into patches of suitable habitat (Benton & Bowler, 2012b). When organisms move between patches, they migrate (Benton & Bowler, 2012b). Migration between patches can happen once in an organism's life as in the case of a young animal establishing a new territory or many times over the life time of the animal (Matthysen, 2012). When enough migration occurs between patches the population dynamics in the patches synchronize and the whole population acts as one. Migration has commonly been explored with computer models (Briggs & Hoopes, 2004). The simplest spatially explicit computer models used to model migration use two patches with either a fraction of the patches migrating or a continuous movement between the patches (Briggs & Hoopes, 2004). These can also be extended to lattices and other spatial patterns (Ben-Zion, et al., 2011).

My question was how migration affected host-parasite population dynamics. The amount of migration can be broken down into three parts: rate of migration, frequency of migration, and form of migration. The fraction of the population moving and time between migration events are other ways migration can happen (Briggs & Hoopes, 2004). Animals are often locked into host-parasite population dynamics and the hosts, parasites, or both can migrate (Briggs & Hoopes, 2004). The rate of migration refers to the fraction of the population that moves, the frequency of migration is the time between migration events, and the form is whether the hosts or parasites move.

Host-parasite interactions are commonly modeled with consumer resource functions (Otto & Day, 2007). Consumer-resource functions are a class of coupled differential equations commonly used in economics, physics, and population dynamics. In my model, hosts were modeled as resources and parasites as consumers. The model monitored the change in the number of the consumers and the resources using the growth rate of resources, the death rate of the resources from interacting with the consumers, the growth rate of the consumers with a conversion term from resources to consumers and, finally the death rate of the consumers. There are more complicated versions for consumer resource functions that have intermediate consumers and additional terms to monitor each interaction (Blasius, 2000). A number of different types of functions have been constructed that take environmental constraints into account in the birth and death rates of the consumers and resources. The way that I made my consumer-resource functions spatially explicit was by confining the simulated population dynamics in two patches. The hosts and/or parasites would periodically interact via migration between the patches.

Many studies have looked at the rate of migration. Between 1974 and 2004, thirty-four analytic and simulation studies were reviewed to understand stabilizing effects on parasite population dynamics (Briggs & Hoopes, 2004). They found stabilizing effects from complex self-organizing spatial patterns (Briggs & Hoopes, 2004). Patches tend to anti-synchronize with some types of model (Briggs & Hoopes, 2004). A later study showed a tradeoff between optimal migration rate and complete synchronization (Arumugam & Dutta, 2018). Another recent migration study examined gene frequencies computing the minimum traveling wave speed for dispersal (Goodsman, et al., 2014). In general, these simulation studies of migration in two-patches and lattices are very difficult to calibrate to experimental and observational data (Ranta & Kaitala, 2006). For this reason, simulated migration in two-patches and lattices has fallen out of favor since the late 1990s and early 2000s (Ranta & Kaitala, 2006). We know that in some models, increased rate of migration increases the faction of experiments and time it takes

to completely synchronize patches (Ben-Zion, et al., 2011). Migration models can be seen as a type of coupled oscillators (Briggs & Hoopes, 2004). A coupled oscillator can have a critical value where the dynamics shift from one type of behavior to another (Rosenblum, et al., 1997). In this model, two Rossler oscillators were found to shift at a critical value from complete synchronization to lag synchronization (Rosenblum, et al., 1997). Migration was set to happen at a fast time scale relative to the predator-prey dynamics so they could use asymptotic solutions to find fixed points in their system (Abdllaoui, et al., 2007). Density dependent rates of migration have been commonly studied as well, where the migration rate varied over the simulations as a function of population density (Abdllaoui, et al., 2007). To address the synchronization behavior in my simulations, I will use only set-rates of migration. I wanted the type of synchronization behavior to be a function of the rate of migration, so I only used set-rates of migration. The time between migration events has been experimented with in the context of invasive species management. The general principle is to increase time between introduction events so that there is more chance to eradicate the invasive species before they have a chance to establish themselves (Kowarik, 1995). Migration form is the least studied of these three aspects of migration that I will be exploring. In the models that have come before, when migration form was specified, it was nearly always parasite only migration (Briggs & Hoopes, 2004). I chose to look at set rates of migration, frequency or time between migration events and form of migration.

There are two types of physical systems, conservative and dissipative. There are consumer resource functions of both types. Conservative systems are common in physics when describing idealized systems with no external forces. A frictionless pendulum would be an example of such a system. A conservative system has a conserved quantity that remains constant for all time. In the example of the frictionless pendulum, the conserved quantity is the total mechanical energy of the system. The properties of the conserved quantity are quite useful in physics and result in the fundamental laws of conservation of energy and momentum. The physical meaning of a constant conserved quantity is that there is an exact value that constrains all interactions so that the conserved quantity remains the same for all time. A conserved quantity is totally dependent on initial conditions. In the example of the frictionless pendulum, the place the bob is released results in a unique trajectory. Even the slightest perturbation from this trajectory must change the total mechanical energy and result in a new unique trajectory and new conserved quantity. Conservative systems cannot have attractors of any kind. This makes stable fixed points, unstable fixed points and limit cycles impossible. This makes conservative system both idealized and very fragile to disturbance. Conservative systems can be accurate models for simple systems when external forces are neglectable, but lose their utility outside of

these very special cases. Very few biological systems can be modeled accurately long term with a conservative system (Strogatz, 2015).

In contrast to conservative systems, dissipative systems include friction and other external forces. A conserved quantity can often be calculated, but its value will not be constant for all time. This loses the utility of the conserved quantity. An example would be a pendulum with friction. As the bob swings it loses mechanical energy to friction and eventually come to rest. The conserved quantity of this system also decays to zero. There is no constant conserved quantity in a dissipative system. Dissipative systems are often nonlinear and more complicated. They are often better fits for complex systems such as biological systems (Strogatz, 2015). The saturating type II system has a density dependent feedback giving it a limit cycle attractor (Wrzosek, 1990). This makes it a better model where there is density dependent fitness (Wrzosek, 1990).

To address my main questions, I contrasted two consumer resources models. Model 1 is a two dimensional version of the Lotka Volterra system and Model 2 is a saturating type II system. There are two major differences between these two systems. First, Model 1 is a conservative system and Model 2 was a dissipative system. Second, Model 1 was idealized and Model 2 reflected environmental constraints. In most aspects, Model 2 is more biologically realistic than Model 1.

Chapter 2: The Model

For the basic construction of the model, I start with two interacting species, a host and parasite. I modeled their population dynamics using a consumer-resource function where the host is the resource and the parasite is the consumer. The interaction of parasite and host in a patch is labeled with a "consumer resource function" in Figure 1. I embed the population dynamics of these two interacting species in a spatially explicit model that includes two patches. I connect the population dynamics of these two patches with periods of migration where a fraction of each population moves from one patch to the other, see purple arrows in Figure 1.

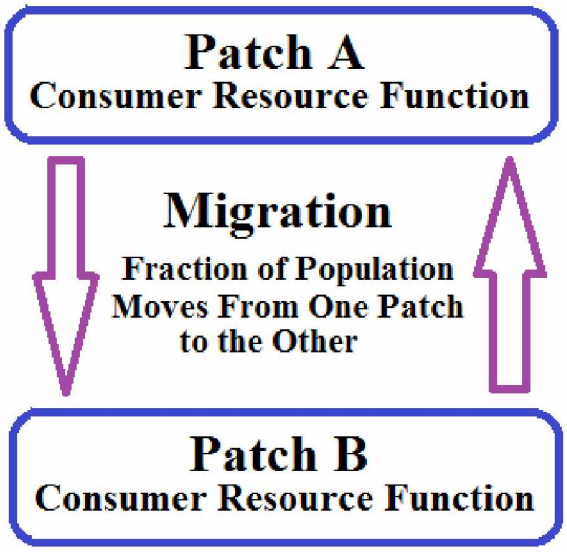

Figure 1: Diagram of the two patch structure of my computer model. Two patches, A and B, run independently with hosts and parasites interacting through a consumer resource function for a set number of time steps, at which time a migration event, purple arrows, occurs where a fraction of the population of each patch moves to the other patch symmetrically.

Below, I describe the two models. The consumer-resource models chosen contrast a conservative system and a dissipative system. Model 1 uses the Lotka Volterra system as the consumer resource function. The Lotka Volterra system is conservative. Model 2 uses the saturating type II system. This system has a feedback term that for some parameter values (see Table 1) make it into a dissipative system with a limit cycle.

Model 1

The Lotka Volterra equations are the simplest equations used to model consumer resource interactions where all birth and death rates of both host and parasite are modeled as linear functions. We model the instantaneous change in the host and parasite population dynamics within a patch using equations 1 and 2,

$$\frac{dH}{dt} = aH - bHP, \tag{1}$$

$$\frac{dP}{dt} = cHP - dP \tag{2}$$

where equation (1) describes the rate of change in host population and equation (2) the parasite population (Strogatz, 2015). The host population is *H* and parasite population is *P*. Linear growth of the host population is determined by the parameter a. The interaction between hosts and parasites resulting in hosts having a death rate caused by the parasites is determined by the parameter *b*. The parameter *c* represents the growth rate of the parasites as they feed on the hosts. The parameters *b* and *c* are related by showing the efficiency of conversion of hosts to parasites. If *b* is greater than *c* many hosts go to feeding one parasite, this would be equivalent to a large parasite eating smaller hosts (more traditionally referred to as predator-prey dynamics). If *c* is larger than *b* then it represents many small parasites feeding on one larger host. The second scenario was the one I explored. Finally, the parameter *d* represents the linear death rate of the parasites. To reduce the number of parameters, I non-dimensionalized this system into equations (3) and (4),

$$\frac{dH}{d\tau} = H - \alpha HP, \tag{3}$$

$$\frac{dP}{d\tau} = \beta HP - \gamma P \tag{4}$$

where equation (3) describes the non-dimensional rate of change in host population and equation (4) the non-dimensional rate of change in the parasite population (Strogatz, 2015). The non-dimenstional parameters have analogous meanings to their dimensional counterparts. The parameter α in equation (3) is constructed from a ratio of *a* and *b* from equation 1 and rescaled from *t* to τ by a constant. Similar transformations involving *a* and *c* or *d* then rescaling to dimensionless time, τ was done for β and γ in equation (4). The relationship between α and β is the same as the relationship between *b* and *c* in equations (1) and (2). I explored a parameter space where β was greater than α so I would generate many parasites from a single host. The values are given in Table 2.

The Lotka Volterra equations are a conservative system. Being a conservative system, the Lotka Volterra system is expected to have conservative behavior. Time series oscillate in the same pattern for all of time with parasite populations tracking the host populations, see Figure 2A. The Lotka Volterra system is restricted to producing centers in phase space, see Figure 2B. No attractors such as limit cycles or stable or unstable fixed points are possible. The most important defining feature of a conservative system is having a conserved quantity that remains constant for all time for a particular initial condition. The conserved quantity for the Lokta Volterra equation is

$$Conserved\ Quantity = lnP - \alpha P - \beta H + \gamma lnH\ , \tag{5}$$

where *P* and *H* are the parasite and host populations, see Figure 2C.

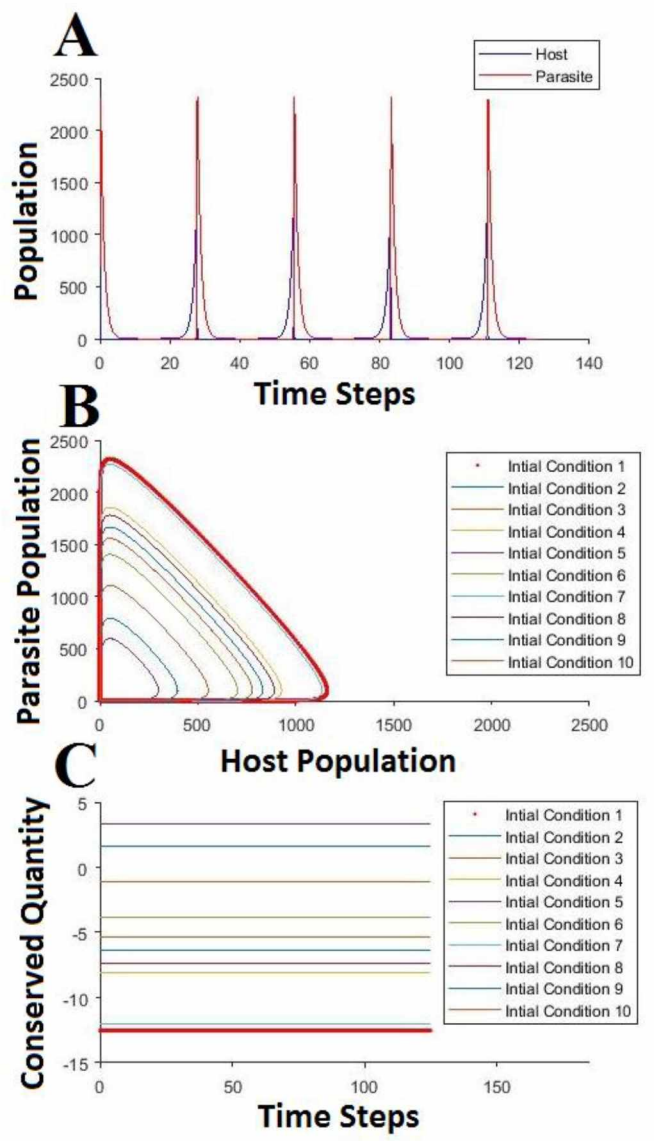

Figure 2: Expected behavior in one patch of The Lotka Volterra equations. In Graph A, only the first initial condition is shown. The time series shows that oscillations in parasite population track oscillations in host population. In Graph B, centers for ten initial conditions are shown in phase space as the loops. Graph C shows the corresponding ten conserved quantities that remain constant for the ten initial conditions used. The thick red line in both the phase space and conserved quantity plots shows the same initial condition to make the point that for every unique initial condition there is a unique phase space center and conserved quantity.

When migration is added to Model 1, this conservative behavior is interrupted. Any perturbation from a given center is expected to result in a new center with a new conserved quantity. Migration acts as a perturbation and the conserved quantity jumps to a new value at each migration

event, see Figure 3. This means that the model as a whole is not conservative. The conserved behavior is only seen between migration events in each non-interacting patch.

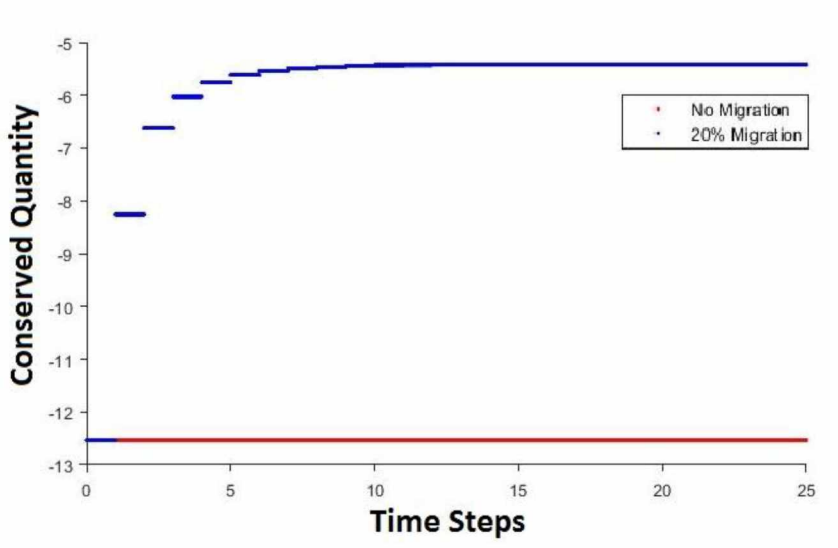

Figure 3: Conserved quantity in Model 1 with and without migration. The red line shows the conserved quantity with no migration stays constant. When migration is added, the blue line, with each migration event, the conserved quantity jumps to a new value where it stays constant until the next migration event.

Model 2

I constructed Model 2 to be a more biologically realistic model that takes density dependence into account in its birth and death rates. The consumer resource function I used is called the saturating type II system. I placed it into the two patch model. The saturating type II system is a dissipative system. It has qualitatively different behavior than the Lotka Volterra system because of density dependent feedbacks in the host's birth rate, host's death rate, and parasite's birth rate. The saturating type II system has a limit cycle for certain parameter values. The coupled differential equations for the saturating type II system are

$$\frac{dH}{dt} = rH\left(1-\frac{H}{k}\right) - \frac{cHP}{a+H}\,, \tag{6}$$

$$\frac{dP}{dt} = \frac{bcHP}{a+H} - dP \tag{7}$$

where equation (6) describes the change in host population density and equation (7) describes the change in parasite population density (Wrzosek, 1990). The first term in equation (6) is the density

dependent birth rate of hosts. The carrying capacity of hosts is *k*. For a full stability analysis and discussion of each density dependent term see the Appendix. The parameter values are given in Table 1.

Table 1: Parameter in Models

Parameters	Values	Description
Model 1		
α	0.01	Death rate hosts from interacting with parasites
β	0.02	Birth rate of parasites from interacting with hosts
γ	1	Death rate of parasites
Model 2		
k	100	Carrying capacity of hosts
a	50	Location of vertical asymptote in second quadrant
b	6	Conversion rate of hosts to parasites
c	4	Strength of host-parasite interaction term
d	4	Death rate of parasites
r	10	Strength of host density dependent birth rate term

The Simulation

I constructed the simulations in MatLab (R2017a, The Mathworks). The code and data used to generate all my results can be found in the Supplemental Files. Within each patch, I solved the consumer resource function for either model using MatLab's built-in differential equation solver, ODE45. This is an optimized Runge Kutta algorithm. I used 50 initial conditions chosen from MatLab's built in Latin Hyper Cube sampler, lhsnorm. These sampled values came in a range from zero to one. To make the initial conditions used for Model 1 and Model 2, I multiplied the values obtained from the sampler by the maximum population for host and parasites for the respective models. I ran these same 50 initial conditions for each form of migration, frequency of migration, rate of migration and model tested.

I have grouped together four time parameters used to control my simulations, see Table 2. First, I ran simulations of host and parasite population dynamics with the two disconnected patches for a length of time called the migration interval. At the migration interval the two patches interacted through migration, and then went back to running independently until the next migration event was called. Second, I set the number of migration events to happen in the simulation as the migration events parameter. Third, I ran my simulations for a set amount of time called the total length parameter. The total length was the product of the migration interval and migration events. Finally, my fourth control parameter was the interruption time and was required by the differential equation solver to set the maximum allowed time step. This was kept the same in all simulations.

I constructed migration events so that a fraction of one patch moved to the other patch symmetrically. Since there were only two patches, the fraction that moved from one patch had nowhere else to go but to the other patch. I controlled the migration rates of hosts and parasites separately. I collected data from migration rates of 0%, 0.1%, 0.5%, 1%, 5%, 10%, 20% and 50%. The time between migration events was called the migration frequency and controlled by the migration interval parameter. I examined two migration frequencies for Model 2. High frequency migration has a migration interval of 1 and low frequency migration had a migration interval of 10. I only examined high frequency migration in Model 1 due to requiring increased simulation time. I constructed three forms of migration: host only, parasite only, and both host and parasite migrating at the same rate.

Simulations were run for a fixed amount of time and then evaluated for synchronization or lack thereof. For migration rates below 5% in Model 1, the simulations needed to be run for 10,000 migration events, but in all other case 1000 migration events was enough. To assess the synchronization

of the patches, the difference between the patches was computed. The difference between the patches was noisy so smoothed using MatLab's built in loess function. This function required a smoothing parameter that I set to 0.05 for all plots. The smoothed difference between the patches always approached a horizontal asymptote within the first half of the run time. The patches were said to be synchronized when the asymptote appeared. I took the mean of 2000 data points from near the end of the simulation, after synchronization had occurred and before artifacts from the smoothing function started. I called this the lag test value. I compared the lag test value to the threshold value. For the two patches to be completely synchronized the lag test value needed to be below the threshold value.

I took the initial conditions that completely synchronized and found the time that it took to drop below the threshold value. This was the threshold time. For constructing plots of the threshold time, I only kept simulations of forms, frequencies, and rates of migration that completely synchronized 20% of the time or more. If complete synchronization happened less than 20% of the time there wasn't enough data for the error bars to be meaningful.

Table 2: Simulation Parameters

Simulation Parameters	Value or Range of Values	Explanation of Parameter
Initial Conditions		
Initial Conditions	[0, 1]	Vector of 1000 initial conditions selected from a Latin Hyper Cube
Time Control Parameters		
Migration Interval	[1, 10]	Time steps between migration events
Migration Events	[1000, 10,000]	Number of migration events
Total Length	[1000, 10,000]	Total length of simulation. The product of Migration Interval and Migration Events.
Interruption Time	0.1	Time steps between integration in loop
Migration Rates		
Host Migration	[0, 0.5]	Host migration rate
Parasite Migration	[0, 0.5]	Parasite migration rate
Threshold Plots		
Threshold Value	1	Threshold value where the difference in population size between patches is approximately the same.
Lag Test	[35,000-37,000, 305,000-307,000]	The mean of 2000 data points at the end of the time series (after synchronization and before smoothing errors) tested about of synchronization.
Smoothing	0.05	Smoothing of difference between plots, this variable was called for my MatLab's inbuilt loess function.

I used Model 2 to understand how migration rate, frequency, and form, affect population dynamics. The critical difference in phase space behavior between Model 1 and Model 2 is the limit cycle. The limit cycle is an attractor so all initial conditions will flow to it. I show this behavior in Figure 4A. As the simulation in run, ten initial conditions denoted as red stars time advance along the green line and eventually come to rest as blue circles on the limit cycle shown as the large red loop, see Figure 4A. To emphasize that the limit cycle is an attractor, I plotted the time series for one initial condition with no migration for the hosts and parasites in one patch, see Figure 4B. After the transients die off, the peak populations of hosts and parasites match that of the maximum population on the limit cycle shown as the black dashed line.

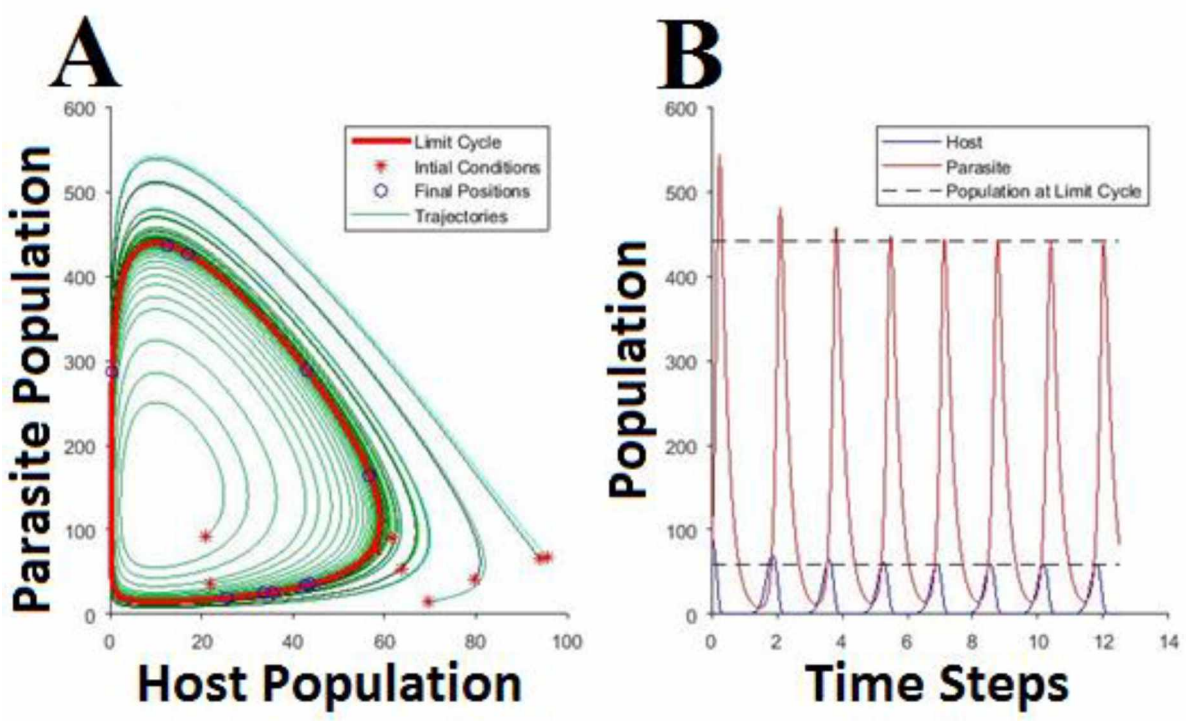

Figure 4: Initial conditions are attracted to the limit cycle in Model 2. In graph A, all initial conditions, denoted as red stars, find their way to the red limit cycle. The endpoints of time series are blue circles that all sit on the limit cycle. Graph B shows the absolute value of the population for one simulation in one patch with no migration. The maximum population of hosts and parasites on the limit cycle is the black dashed line. The transient behavior of the simulations die off as the limit cycle is reached with peaks progressively approaching the maximum population on the limit cycle.

Vetting the Simulations

I used the Lotka Volterra system to vet the differential equation solver in one patch. The Lotka Volterra system showed the expected behavior in the time series, phase space and conserved quality plots for a single patch with all initial conditions. After this first version, the one patch model, was shown to work, I constructed a second version with two patches run side by side. I had the expectation that the patches would be identical and match the one patch model run for the same initial condition. A third version of the model was constructed with a migration step. This migration step was set to zero and was also expected to behave exactly like the patches that had been run before. Finally, I added an if-statement to allow modification in the amount of time between migration events. This version I called 3.5. Again migration was set to zero with the expectation that it would behave exactly like the other versions that had no migration. I plotted all the versions for both Model 1, (see Figure 5A) and Model 2, (see Figure 5B) on top of each other to show that the behavior was identical. Finally the special case of two identical patches was examined by setting the same initial condition in both patches with non-zero migration. The expected behavior of no difference between the patches was observed for both Model 1 and Model 2. I tested the threshold plots with step functions and sine waves and found they had expected threshold times or lack of.

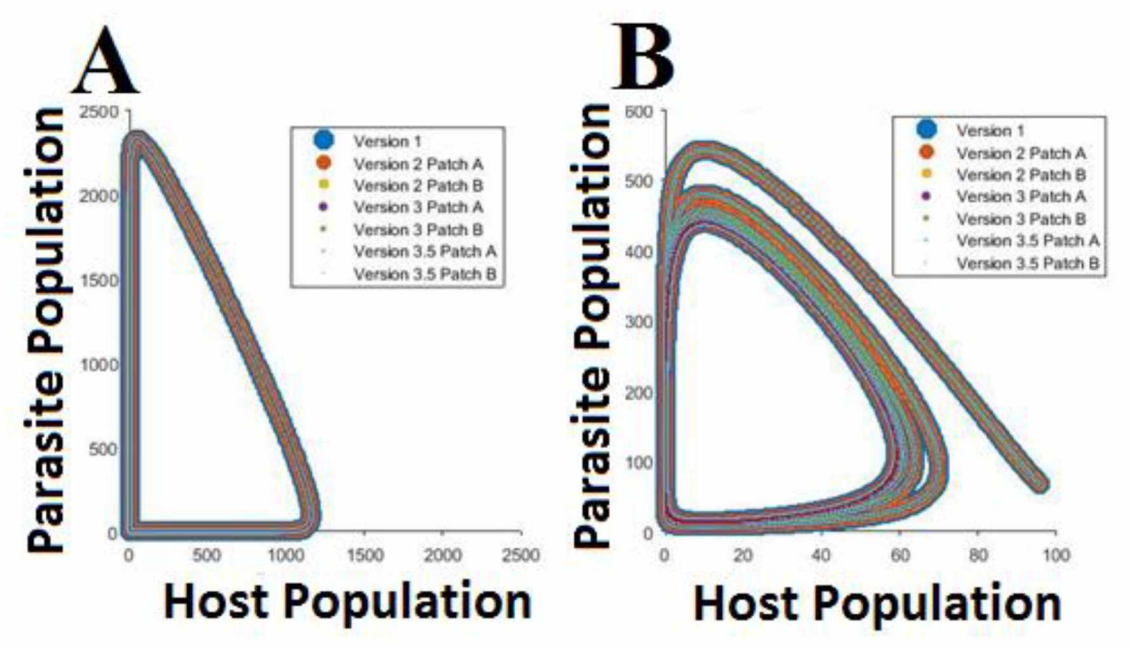

Figure 5: Unit tests for simulation of Model 1 and Model 2. The unit tests for version 1 through 3.5 for both Model 1 and Model 2 have the expected behavior. All versions of both Model 1 (Graph A) and Model 2 (Graph B) produce the same phase space plot given the same initial conditions so plot on top of each other.

Chapter 3: Results from Model 1

I aimed to understand how simulation of migration rate and form affected population dynamics in Model 1. I examined the plots of the smoothed difference between the patches and constructed plots of both the fraction to completely synchronize below the threshold value and plots of the time it took to

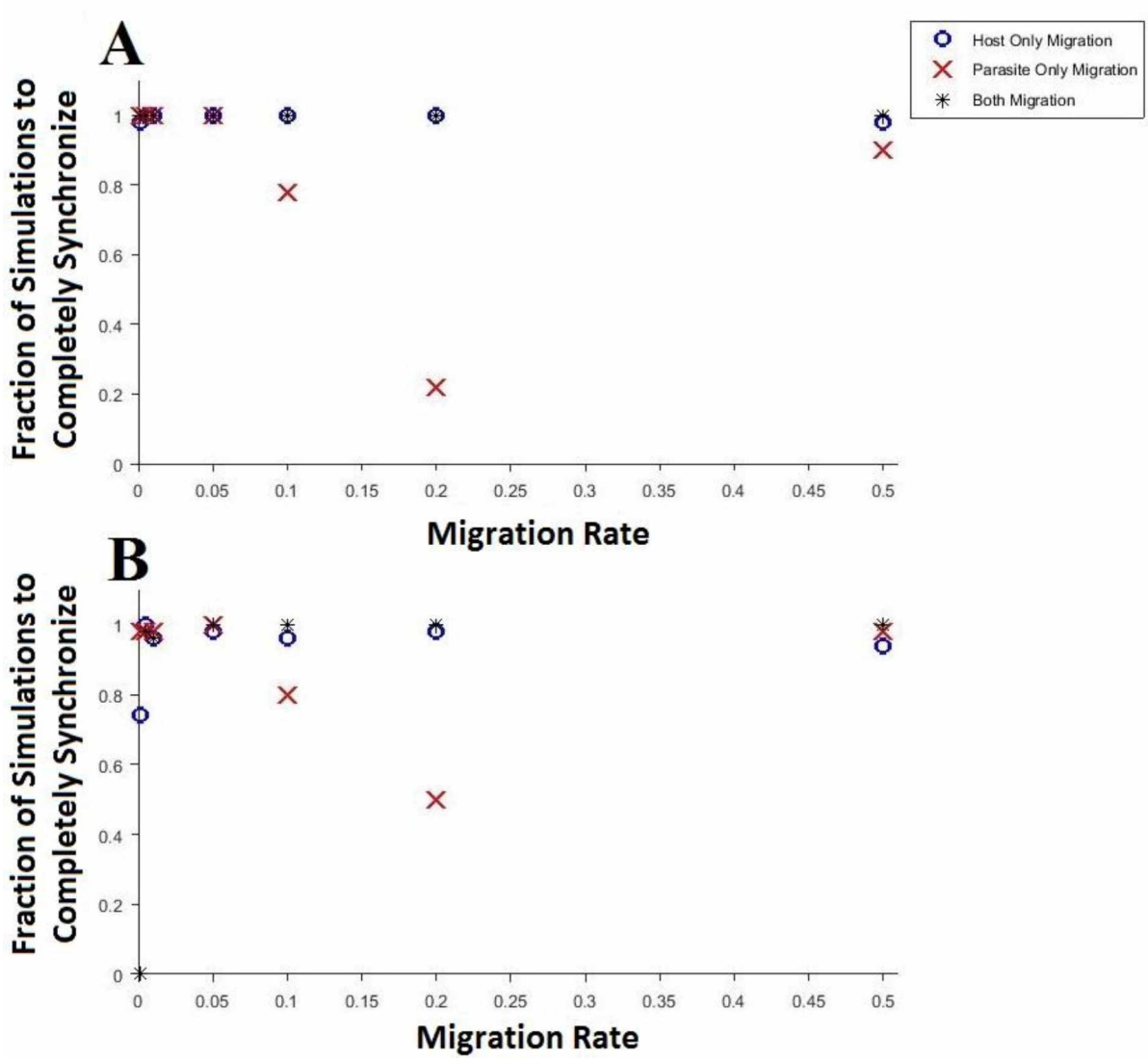

Figure 6: Fraction of intial conditions in Model 1 to completely synchronize. The fraction to completely synchronize for the hosts in panel A and parasites in panel B for Model 1. The majority of forms and rates of migration completly synchronize for all or nearly all intial conditions with fractions to synchronize at or near 1. There are a few exceptions such as the 10% and 20% migration rates for parasite only migration, denoted as the red xs well below 1.

reach the threshold value for the initial conditions that completely synchronized. Where the fraction to completely synchronize was below 20%, the time to reach the threshold value was not plotted due to the small sample size.

I tested the fraction of fifty simulations to completely synchronize for each initial condition and for each parameter combination of migration form and rate for both host (Figure 6A) and parasites (Figure 6B). The fraction of simulations to completely synchronize was measured by whether the smoothed difference in population size between patches fell below a threshold value. I found that nearly all simulations of form and rate of migration resulted in nearly all initial conditions completely synchronizing. There were a few exceptions. Simulations of parasite only migration at migration rates of 10% and 20% results in lower fractions of synchronization in both the host and the parasite populations. I also observed a lower fraction of synchronization in the parasites for the lowest migration rate of 0.1% with host only migration and with both host and parasite migrating.

Simulations with changes in migration rate resulted in two possible threshold times. For simulations with low migration rates there was a longer times to synchronize, approximately an order of magnitude longer than the threshold time for simulations of high migration rates. There appeared to be a sharp transition between these two times to synchronize that depended on both migration rate and on migration form. This transition for both the host and the parasite occurred between the migration rates of 1% and 5% for hosts only migration and between 5% and 10% for parasite only and both migration. The greatest variance was observed on simulations of parasite only migration where the smallest fractions completely synchronized and for simulations done with 50% migration rate for host only migration in hosts which had many very low threshold times. The time it took for the populations in the patches to completely synchronize was measured by recording the time when the smoothed difference in population size between patches fell below a threshold value (see Table 2). This threshold value was relatively small and used to approximate when the difference between the patches was small enough to be ignored. The difference between patches was unlikely to reach exactly zero because of the approximations made using the differential equation solver. Only parameter combinations of migration rate and form that synchronized at least 20% of the fifty simulations done were used to find the time to synchronize the patches. The overall patterns in parameter combinations for simulations of the hosts and the parasites were very similar as can be seen by comparing Figure 7A and 7B. Error bars show the 5% to 95% confidence interval for the times to threshold. For simulations of large migration rates, after the transition to the lower threshold value, the form of migration becomes distinguishable with no

overlapping error bars. I observed that both migrating has the longest threshold times with parasite only migration having the shortest threshold times and host only migration being in the middle until 50% migration where host only and parasite only migration become indistinguishable (Figure 7).

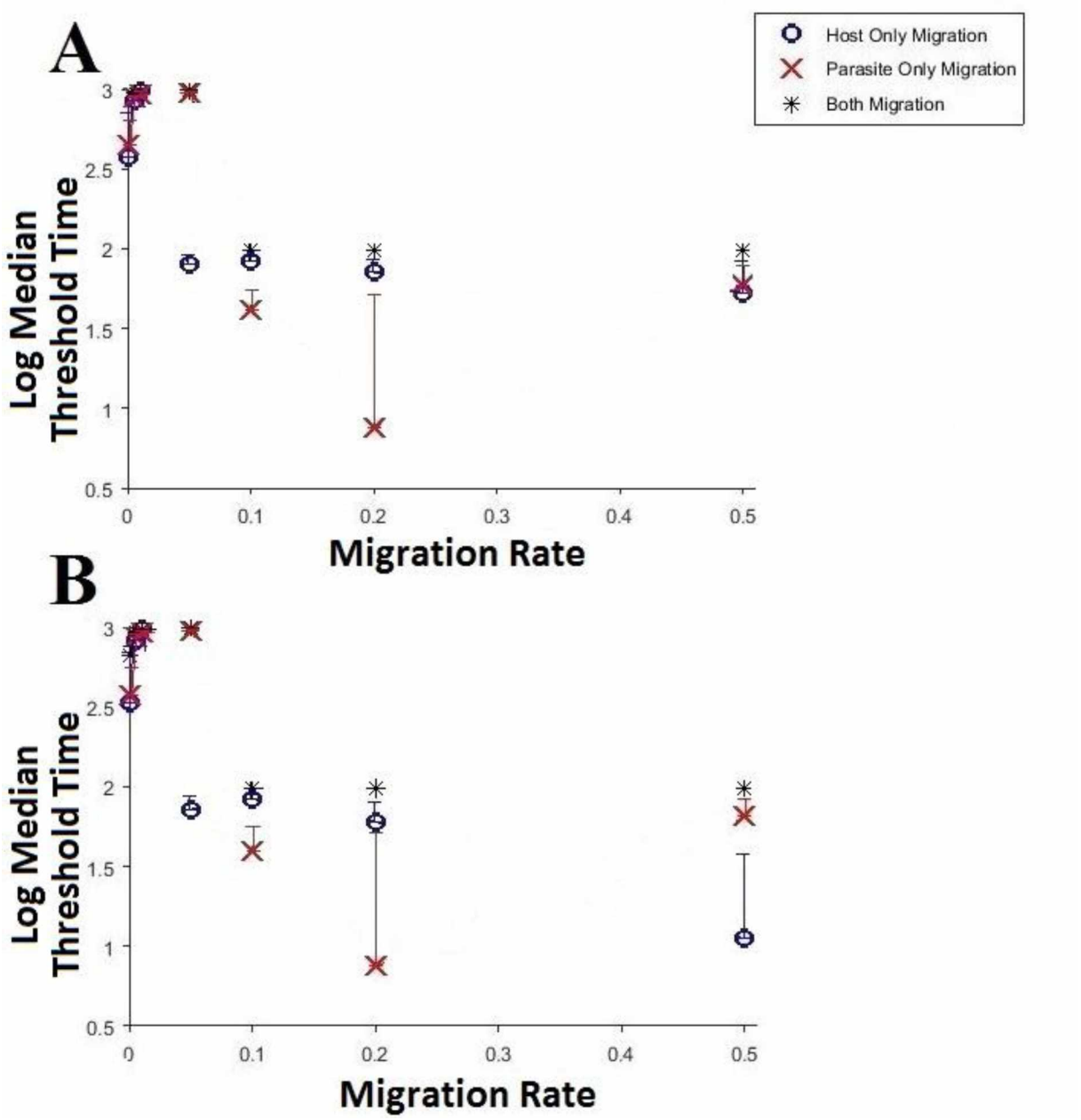

Figure 7: Threshold times by migration rate for Model 1. The time to reach the threshold value for all forms and rates of migration that completely synchronized 20% of the time for Model 1. Error bars show the 5 to 95% confidence interval on the time to synchronize as measured by the time the simulation took to reach the threshold value. Panel A shows the hosts and panel B shows the parasites. There is shift in the threshold times observed between low and high migration rates. Low migration rates have a high median threshold time that is about one order of magnitude higher than the median threshold values for high migration rates. The place where this transition occurs depends on migration form. The transition from high threshold time to low happens between 1% and 5% migration rate for host only and between 5% and 10% for parasite only and both migration. At migration rates of 10% and 20% the form of migration becomes distinguishable. I observed that simulation where both migrate synchronize later than host only migration, with parasite only migration reaching the threshold first although having a large variance. Threshold times between zero and one have been rounded to one for clarity on the log base 10 scale.

Chapter 4: Results from Model 2

I used Model 2 to understand how migation rate, frequency, and form affected population dynamics in a more realistic biological context. I analyzed this model using the fraction to completely synchronize and the time that it took the populations to synchronize. I measured this time as the time when the smoothed difference between the patches fell below the threshold value, see Table 2. Most obvious, the fraction of simulations to completely synchronize was far lower in Model 2: compare Figure 6 and Figure 8. Relatively few rates, frequencies and forms saw all intial conditions completely synchronize, with the overall pattern in host and parasite being similar: compare positions of markers on panel A and B of Figure 8.

Second, as a general trend, the fraction of simulations to completely synchronize was larger for high migration rates. I did notice some exceptions to the pattern that larger fractions of simulations synchronized for high migration rates. A higher fraction of simulations completely synchronized for simulations run with high frequency parasite only migration at 1% and 5% with all simulations of intial conditions completely sychronizing, see the red triangles near 1 in Figure 6. Third, I compared high frequency migration to low frequency migration (Figure 8, compare circles, triangles, and squares to star, dot, x). High frequency migration were always above low frequncy migration. High frequency migration is more likely to completely synchronize. Finally, I obsevered the same general pattern in threshold times for migration rates at ot over 10% in each form of migration. The highest fraction to completely synchronize was both migrating followed by parasite only migration. The lowest fraction to completely synchronize is host only migration, see Figure 8.

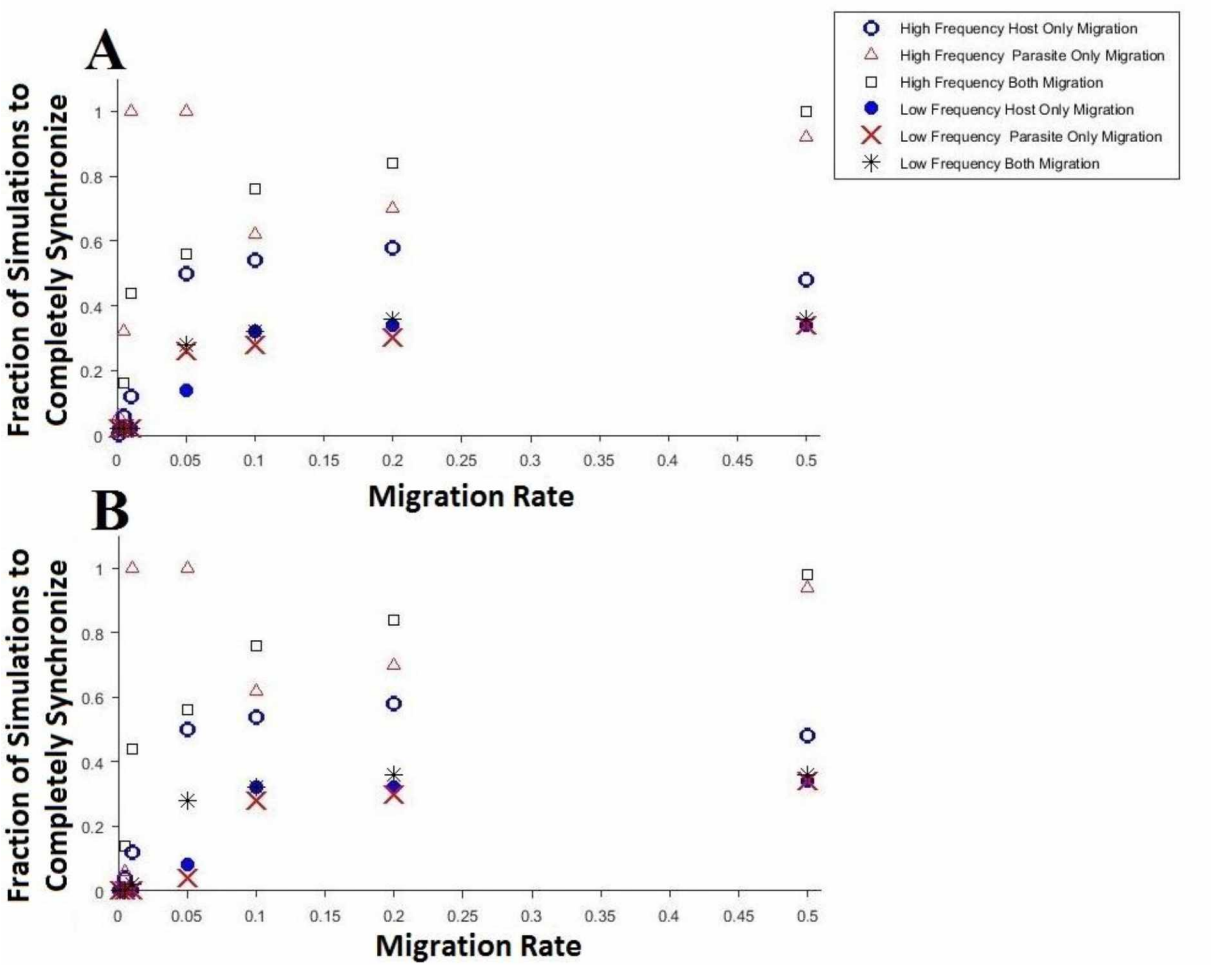

Figure 8: Fraction of initial conditions in Model 2 to completely synchronize. The fraction to completely synchronize for all frequencies forms and rates of migration for Model 2 for both the host (panel A) and parasites (panel B). Many low migration rates do not completely synchronize often enough to be used to calculate the time to reach the threshold value. Migration frequency has the next greatest effect on complete synchronization with high frequency migration completely synchronizing more often than low frequency migration. Finally form of migration had a smaller effect making both migration synchronize completely more often than parasite only and finally host only migration.

I calculated the time to reach the threshold value for all forms, frequencies and rates that completely synchroized more that 20% of the time. I used this to constuct plots of the time it took to reach the threshold value, compare Figure 9 with Figure 7 (Model 1). The host and parasites have approximately the same behavior for high frequency migration, flat lines at the same threshold time (Figure 9C, D). For low frequency migration the parasites have far more variance in threshold time than the hosts (Figure 9A, B). I observed that low frequency migration had about an order of magnitude greater threshold times than high frequency migration. The only place where form of migration appeared to have an effect was on the parasites in low frequency migration, see panel B. There I observed that both migration reached the threshold later than host only migration. Parasite only migration had the shortest median time to reach the threshold value and had the greatest varance.

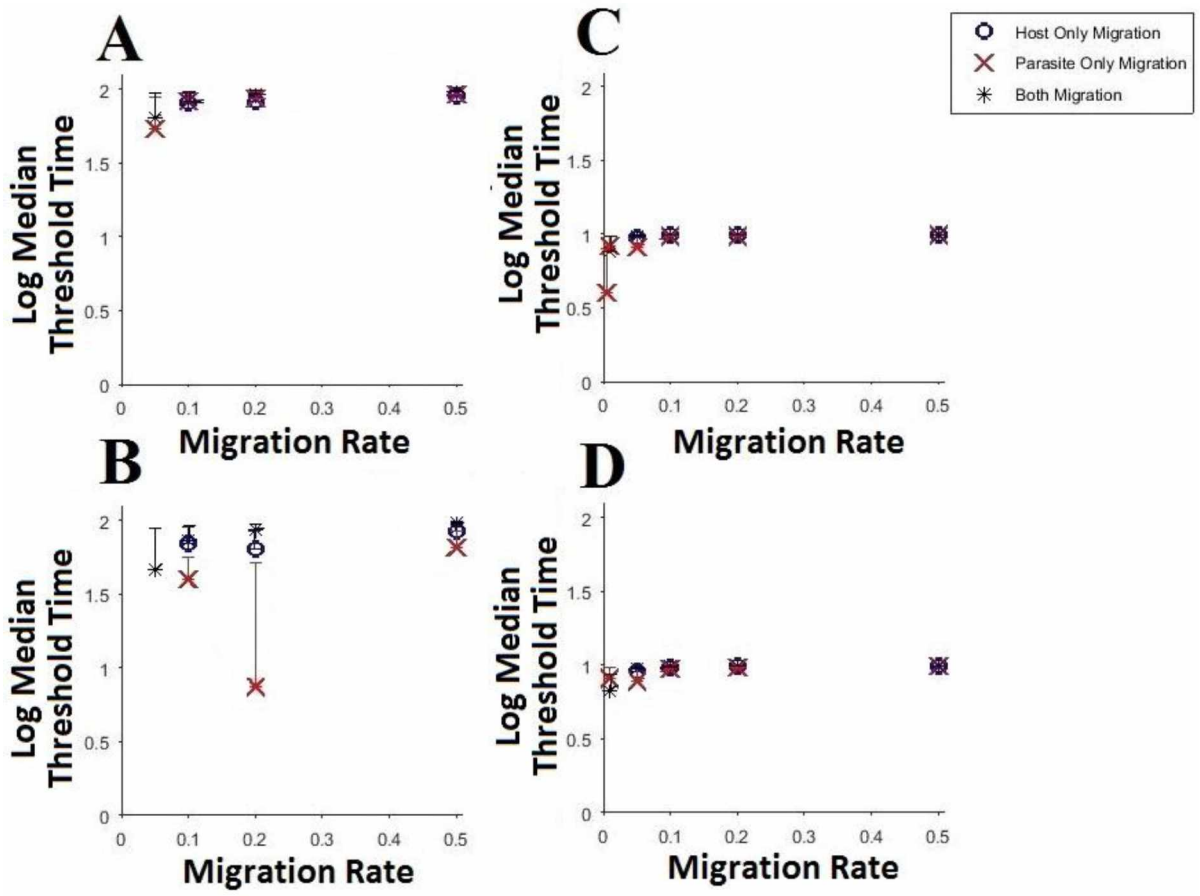

Figure 9: Threshold times by migration rate and frequency for Model 2.The time to threshold for Model 2 for both frequencies and for both the host and the parasite. Error bars show the 5 to 95% confidence interval on the time to synchronize as measured by the time the simulation took to reach the threshold value. The left column has low frequencies of migration and the right column has high frequencies of migration. The top row is host and bottom row is parasites. From this we can see that low frequency migration takes about an order of magnitude longer to completely synchronize than high frequencies of migration. The migration form has no notable effect except on the low frequency parasites in panel B where both migrating reaches the threshold later than host only migration and finally followed by parasite only migration. The greatest variance is seen on this panel. Threshold times between zero and one have been rounded to one for clarity on the log base 10 scale.

Finally, I compared Model 1 and Model 2. Model 1 was run with high frequency migration so I compared it only to Model 2 high frequency migration simulations. I plotted both the hosts and parasites for each of the three forms of migration (Figure 10A host only, 10B for parasite only, and 10C both migrating.) The points for hosts and parasites for each of the two models end up closer to each other than points for the other model. Model 1 normally reached the threshold about an order of magnitude later than the Model 2. I observed this trend with host only migration and both migration (Figure 10A, C). For parasite only migration in Model 1 at a migration rate of 20% the threshold value of Model 1 dips below Model 2 with large error bars. I believe this to be the result of the low fraction to completely synchronize at this migration rate and form, see Figure 6 in Chapter 3.

To summarize, migration rate had a strong effect on the fraction of Model 2 to completely synchronize, but had little effect on Model 1. The context of this result comes from the difference between having an attractor and not. Migration rate also created a transition in threshold times in Model 1, but did not do this in Model 2. This could be because Model 2 did not have enough completely synchronized low migration rates to show the transition in threshold times. Migration frequency was only examined in Model 2, but showed that high frequency migration is more likely to completely synchronize and at a lower threshold time. Finally, migration form has a small effect on some migration rates and frequencies with both migrating more likely to completely synchronize and have a larger threshold time. The fraction to threshold is less affected by host only or parasite only migration with Model 1 and Model 2 showing opposite behavior. In Model 1 host only migration completely synchronizes more often than parasite only whereas in Model 2 this trend is reversed. Parasite only migration tends to have the shortest times to threshold and greatest variance in both models.

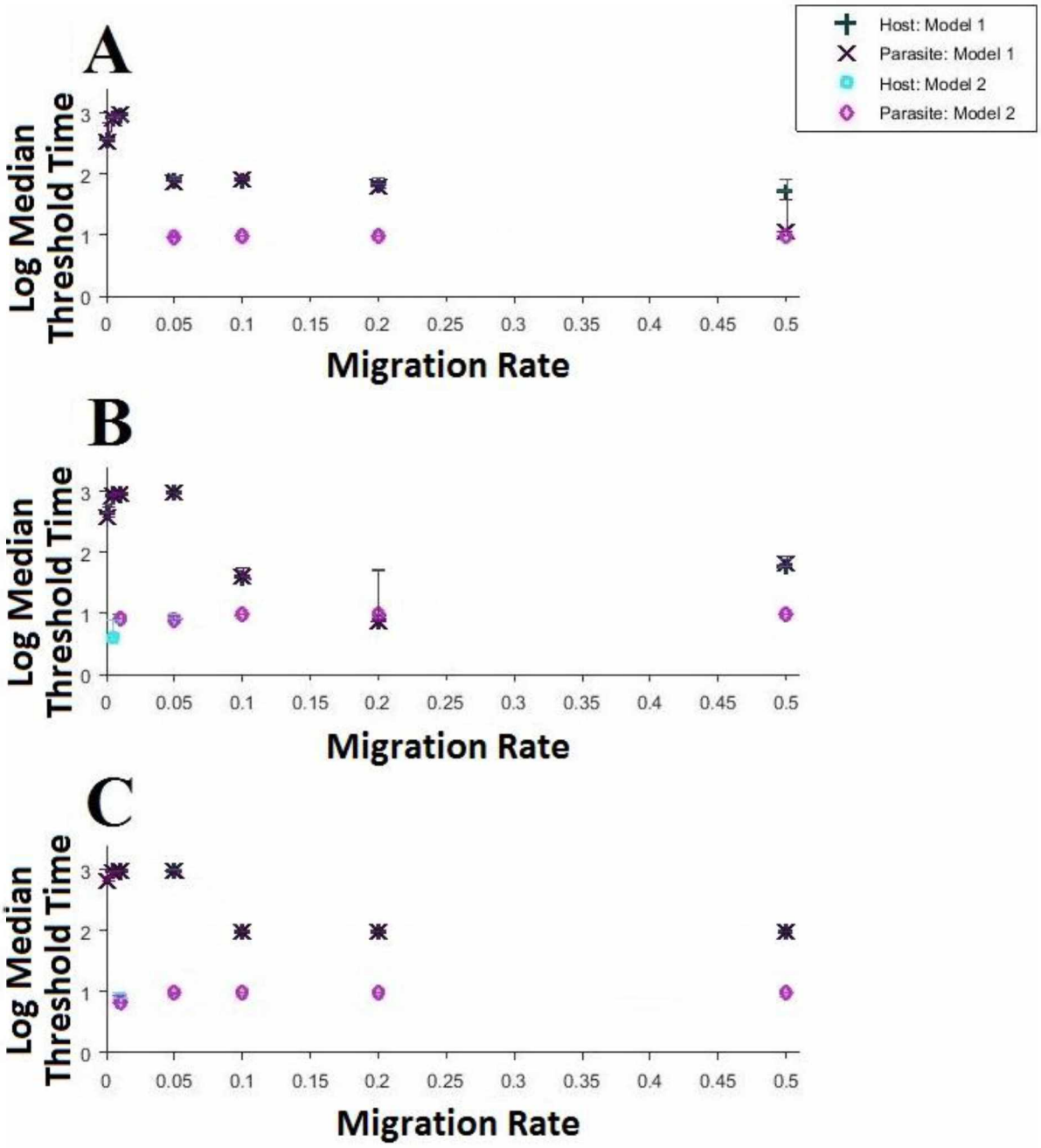

Figure 10: Comparison of threshold times between Model 1 and Model 2. Comparing Model 1 and Model 2 shows that Model 1 tends to reach the threshold value about an order of magnitude later than Model 2. This is seen clearly in panel A and panel C where host only and both migrating approach flat lines that are about an order of magnitude apart for migration rates of 10% or greater. For low migration rates for both migrations seen in panel C, there is a greater difference since Model 1's threshold time is an order of magnitude higher for low migration rates and Model 2 completely synchronized enough to be plotted. Finally panel B has the same trend, but at 20% Model 1 appears to dip below Model 2. This is like the result of relatively low fraction to completely synchronize for this rate and form of migration. Error bars show the 5 to 95% confidence interval on the time to synchronize as measured by the time the simulation took to reach the threshold value. The large error bars indicate that this is likely an anomaly. Threshold times between zero and one have been rounded to one for clarity on the log base 10 scale.

Chapter 5: Discussion

My original question was how migration affected host-parasite population dynamics. For the more biologically realistic Model 2, I found that increased migration rates increased synchronization across space. Higher migration rates led to synchronization more quickly in Model 1. Simulations done with model 2 only synchronized at higher migrations rates. I observed that high frequency migration synchronized patches more often and more quickly than low frequency migration. The form of migration, host versus parasites, had a smaller effect. When both host and parasite migrated, patches synchronized more often but it took longer than when only one species migrated. The fraction to completely synchronization between host only and parasite only migration depended on the model used. In the more biologically realistic model, Model 2, parasite only migration completely synchronized faster and more often than host only migration.

Most studies trying to understand how migration rate, frequency of migration, and form of migration affect population dynamics use computer simulations, but there have been observational and experimental studies as well (Briggs & Hoopes, 2004). For example, Dey & Joshi (2006) calibrated a computer simulation using *Drosophila.* The animals were kept in two separate enclosures where a fraction of the population was regularly exchanged (Dey & Joshi, 2006). The experimental results were very sensitive to initial conditions but making the experiment match the two patch simulation could be done (Dey & Joshi, 2006). The improvement of technology in the early 1990s led to many analytic or agent-based studies of coinheritance between metapopulations (Briggs & Hoopes, 2004). These studies examined density dependent migration or rate of migration. Frequency and form of migration were rarely examined and not as explicit goals of the research. Many models had continuous migration rates so frequency was irrelevant. If the form of migration was given, then it was nearly always parasite only migration (Briggs & Hoopes, 2004). Parasite only migration was chosen for the biological assumption that parasites are more virulent than hosts so more likely to cause a greater impact on simulation results (Briggs & Hoopes, 2004).

Understanding population dynamics of synchronization can help us understand extinction risk (Ben-Zion, et al., 2011). When two patches synchronize their population dynamics, a natural dip in population size can take the entire global population below the extinction threshold where the total population is no longer viable. Synchronization behavior can wipe out an entire population and not just a single patch. When populations are separated and lack regular migration they are unlikely to be

synchronized. This means that when one patch is low while another patch has a higher population, the higher population patch can repopulate the lower population patch if the lower population patch goes extinct while it is at its low point.

Migration rate affects population dynamics up to a point. From my results, increases in migration rate of 10% or greater have a small effect on the fraction to completely synchronize and no effect on the time it took to completely synchronize. Low migration rates either don't completely synchronize or took much longer to completely synchronize; this was mostly observed in Model 2 (Figure 8). The change in behavior from simulations done with low rates of migration and simulations done with high rates of migration happened at a critical value of migration rate shown weakly in Model 2 but quite strongly shown in Model 1 (compare Figures 7 and 8). Finding where this shift in behavior from low and high migration rates happens could be important information to have about real populations experiencing migration. The rate of migration is an important variable to understand and there can be a very large shift in the population dynamics with a small change in migration rate near this critical value (e.g. Figure 7 a shift in threshold times based on migration rate).

Simulations of high frequency migration resulted in quicker and more frequent synchronized patches. The amount of time between migration events matters greatly since when populations completely synchronize they are at a higher chance of global extinction. Both the faster synchronization and higher fraction to synchronize work together to make higher frequency migration more dangerous to a population than low frequency of migration. From my results, increasing the time between introductions would reduce the chance of two patches completely synchronizing and delay the process of complete synchronization.

When both the host and parasite migrate, patches synchronize more often but take longer to do so. This means that if both species are migrating, it will take longer for the population to act as one. This might provide land managers more time to manage consequences but those consequences could be more extreme. When only the host or only the parasite migrates the fraction to synchronize and threshold times were different for the two models. For the more biologically realistic model, Model 2, the parasite only migration synchronized more quickly, implying parasites migrating could be more threatening to a population than hosts migrating.

Applications to Biogeography

Animals in host-parasites relationships on the mainland can be separated when moving to islands (Hoddle, 2002). The host and parasite can also have different rates of arrival when dispersing to islands (Hoddle, 2002). In the theory of island biogeography, there are two parameters that determine the number of species present (Audesirk, et al., 2009). First is the size of the island and second the distance the island is from the mainland (Audesirk, et al., 2009). To some extent each of these parameters affects the migration and extinction rates on islands, but as a general principle larger islands have lower extinction rates and islands further from the mainland have lower migration rates (Audesirk, et al., 2009). From my work a third parameter, the form of migration could also affect the number of species present.

My results can be used to make predictions about how migration rate, frequency and form are likely to affect colonization of islands. The rate of migration causing complete synchronization is not likely to be biologically relevant to island biogeography, but the frequency and form of migration could have effects. For an island to experience a population turnover of a high fraction, 10% or greater, it would need to be so near the mainland that it would likely be considered a part of the mainland, the most likely migration scenario related to island biogeography migration frequency. From looking at my results for frequency of migration, I would predict that if a large turn over in population was to occur a few times in short succession, it could result in the island population completely synchronizing its population dynamics to the mainland in a relatively short time. Small numbers of colonizers may arrive at different time intervals depending on how close an island is to the mainland. Since high frequency migration resulted in higher fractions to completely synchronize and faster threshold times, it would be expected that islands close to the mainland would have population dynamics that look more similar to the mainland. They may even be completely synchronized to the mainland populations with rates of migration as low as 5% with high frequencies of colonization.

Migration form might also have an effect on population dynamics observed on islands. Invertebrates and other small crop pests tend to be able to spread farther from the introduction point (Hoddle, 2002). Parasites are also often much smaller than hosts so are more likely to be passively dispersed than hosts over longer distances (Matthysen, 2012). This would mean that parasite only migration is more likely than host only migration in the environment. Parasite only migration between island and mainland could cause faster complete synchronization in population dynamics between the island and mainland than host only migration. My main prediction would be that parasite only migration

would tend to drive population dynamic on islands *further* from the mainland to synchronize completely to mainland population dynamics *faster and more* often than host only migration in the same situation. This would mean tracking the distribution of parasite dispersal would likely be more meaningful than host dispersal when trying to understand population dynamic on islands.

Directions for Future Research

It should be noted that in addition to large amounts of migration, patches can also synchronize through the Moran effect (Ranta, et al., 1997). The Moran effect happens when the populations synchronize because of the outside environmental conditions driving all local population dynamics to act alike even with little to no migration between patches (Ranta, et al., 1997). An example is in the Canadian Arctic, where spatial synchronization between lynx and hare population dynamics is seen over tracts of land too large for migration to account for the synchronization observed (Ranta, et al., 1997). Environmental conditions appear to be the driving force (Ranta, et al., 1997). Seasonal effects can force a system to completely synchronize (Arumugam & Dutta, 2018). Although the Moran effect can be an important consideration in observed patterns, I only looked at rates of migration. By extending the model to include external drivers like environmental conditions could have more biologically relevant information may be present. One method to expand my model would include placing oscillating values for one of the control parameters in Model 2. This would make the limit cycle attractor change sizes as a proxy for a changing exterior environment, thereby simulating the Moran effect.

Much research has been done on spatial dynamics in biology. Theories have been developed to describe these dynamics. I list a few examples in this paragraph. Outbreaks of insects spread out from the introduction point (Strogatz, 2015). Also, the pattern of how alleles spread, specially the on the edge of an uninhabited environment is well known (Goodsman, et al., 2014). Both of these examples can be modeled as a spreading chaotic wave on a lattice (Briggs & Hoopes, 2004). Networks and lattices have also been commonly modeled resulting in patterns in synchronization (Briggs & Hoopes, 2004).

Synchronization between patches and coupled oscillators have been looked at in many studies in nonlinear dynamics, economics, and population dynamics (Briggs & Hoopes, 2004). The simplest form of complete synchronization occurs where the patches or oscillators show the same behaviors after equilibrium is reached (Volos, et al., 2012). Complete synchronization can happen in any coupled system, but it is not the only way synchronization can occur (Volos, et al., 2012). Where there are limit cycles or other attractors, phase lags and other more exotic chaotic dynamics can stabilize at equilibrium (Volos, et al., 2012). The phase transitions between different forms of synchronization for a system can

be found through estimating and analyzing the Lyapunov exponent (Rosenblum, et al., 1997). These other forms of synchronization can be important. Lag synchronization was found to have a stabilizing effect on the global population in spatially explicit populations (Ben-Zion, et al., 2011). When one patch's population is low another patch's population will be high allowing repopulation through dispersal (Ben-Zion, et al., 2011). In that study, neighboring patches anti-correlate completely resulting in neighboring patches, reaching the maximum and minimum populations at the same time (Ben-Zion, et al., 2011). In my study, I chose to only look at complete synchronization due to computational time and because complete synchronization has been found to increase the likelihood of global extinction (Ben-Zion, et al., 2011). The reason for this is that all patches reach the population lows at the same time. There are good biological reasons to look at other forms of synchronization.

At a population level, lag synchronization can be important for recharging populations. Lag synchronization means that when one patch has a low population, another one has a high population; in this case, the high population patch can repopulate the low population patch increasing the stability of the population (Ben-Zion, et al., 2011). This implies for lag synchronization in my model could be important in understanding the stability of populations in my model. The patches that did not completely synchronize were observed to come into other forms of synchronization such as phase or lag synchronization. Unfortunately, I did not quantify this in my results. Lag synchronization could be quantified by finding the average difference between the patches after the model had come to equilibrium. Equilibrium could be found by finding where the smoothed difference between the patches reaches a constant value. There also might have been other more exotic forms of synchronization. These could be found by estimating the Lyapunov exponent and constructing a phase diagram for the system. Examining the type and amount of lag synchronization between patches as a function of rate, frequency, and form of migration, would be important in understanding the community level population dynamics and stability of the global population.

Only one limit cycle was explored in the saturating type II system. This meant only one type of host-parasite population dynamics was explored in Model 2. With different control parameters, see Table 1, different limit cycles could be formed in each patch and represent different host-parasite population dynamics interacting via migration. There are also parameter values that come with a stable fix point which would represent population dynamics stabilizing to a fixed size, such as a population reaching a carrying capacity and staying there. Population dynamics in different patches could be different because of different external conditions (Ranta, et al., 1997). Exploring these other parameter

regions could be useful in understanding how the mixing of population with different population dynamics is affected by form, frequency and rate of migration.

Both patches were treated as having the same kind of population dynamics between host and parasite. The parameters that controlled the place in phase space where the centers in Model 1 or the limit cycles in Model 2 would appear were the same. This is a very special case analogous two populations mixing between two identical islands. In the real world, two migrating populations are likely to have different population dynamics called geographical mosaic and be modeled with different parameter values in each patch. Testing empirical geographic mosaic of coevolution appropriately is hard (Gomulkiewicz et al., 2007). Careful documentation of reciprocal and non-reciprocal selection across the range of interaction is needed with an understanding of remixing through gene flow, drift, metapopulation dynamics and mutation (Gomulkiewicz et al., 2007). How migration effects the interaction of the patches with different population dynamics is unclear in my model. It might be expected that the different limit cycles would merge into a single combined limit cycle for the two patches as the centers were informally observed to do in Model 1, but it will need to be tested. Also more complicated patch dynamics could be explored such as multiple patch dynamics.

Conclusions

These results have implications for island biogeography, and lead to the prediction that parasites would be more likely to drive the population dynamics on islands further from shore to look like the population dynamics on the mainland. This effect comes from contrasting the case of host and parasite migration. I found high frequency migration to have the greatest impact on island biogeography, because it supports literature that says that regular introductions are more likely to establish populations (Hoddle, 2002).

Appendix

In Model 2 the coupled differential equations used are the saturating type II system (see equation 6 and 7). They are similar to the Lotka Volterra system, but have slightly different units by convention (Wrzosek, 1990). It is defined in terms of population density per unit area and not in terms of the pure population number (Wrzosek, 1990). This difference doesn't change the qualitative results because population size scales linearly with population density. The main interest of this study is the center behavior, not the exact units of the equations. This unit difference should have no effect on the code that is run (Blanchard et al., 2006).

In the saturating type II system, there are two type of density dependent terms. First, the host growth term in the host equation is a carrying capacity term. Second the host-parasite interaction terms in both the host and parasite equations have a saturation term. I will go through how this density dependent terms work.

Model 2 Derivations of Carrying Capacity Term

The graph in Figure 11 has the intercept between zero and birth rate term for hosts, this is the carrying capacity, *k* (Strogatz, 2015). If we examine host density values less than *k*, this term has positive values resulting in the host population density growing, while at host density values more than k, this term has a negative value and results in a host dead rate. The host growth rate is density dependent, populations of hosts will always be increasing or decreasing unless exactly at the carrying capacity. The carrying capacity term is

$$rH\left(1-\frac{H}{k}\right). \tag{8}$$

When the value of H is the host population, r is the growth rate, and *k* is the carrying capacity.

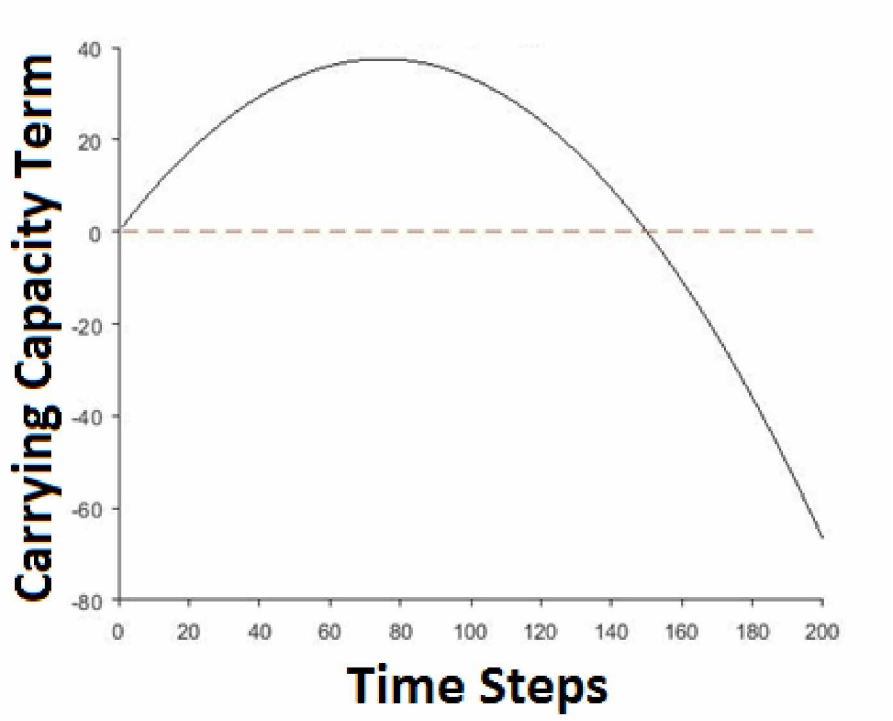

Figure 11: The carrying capacity in the saturation type II equations. The carrying capacity term is plotted to show how the growth rate term works for the first term of equation (6). There are positive growth rates above the red dashed line and negative below. The intersection happens at the value of *k*, the carrying capacity.

Model 2 Derivations of Saturating Term

The second term in equation (6) shows the density dependent consumption of hosts by parasites. Similarly the first term of the parasite equation shows the same density dependent behavior with *b* the conversion rate of hosts to parasites. The effect of the density dependent death rate term in equation (6) (and density dependent birth term in equation (7)) ,

$$\frac{cHP}{a+H}\Big|_{c=1,P=1} = \frac{H}{a+H} = \frac{1}{a+H} * H \ , \tag{9}$$

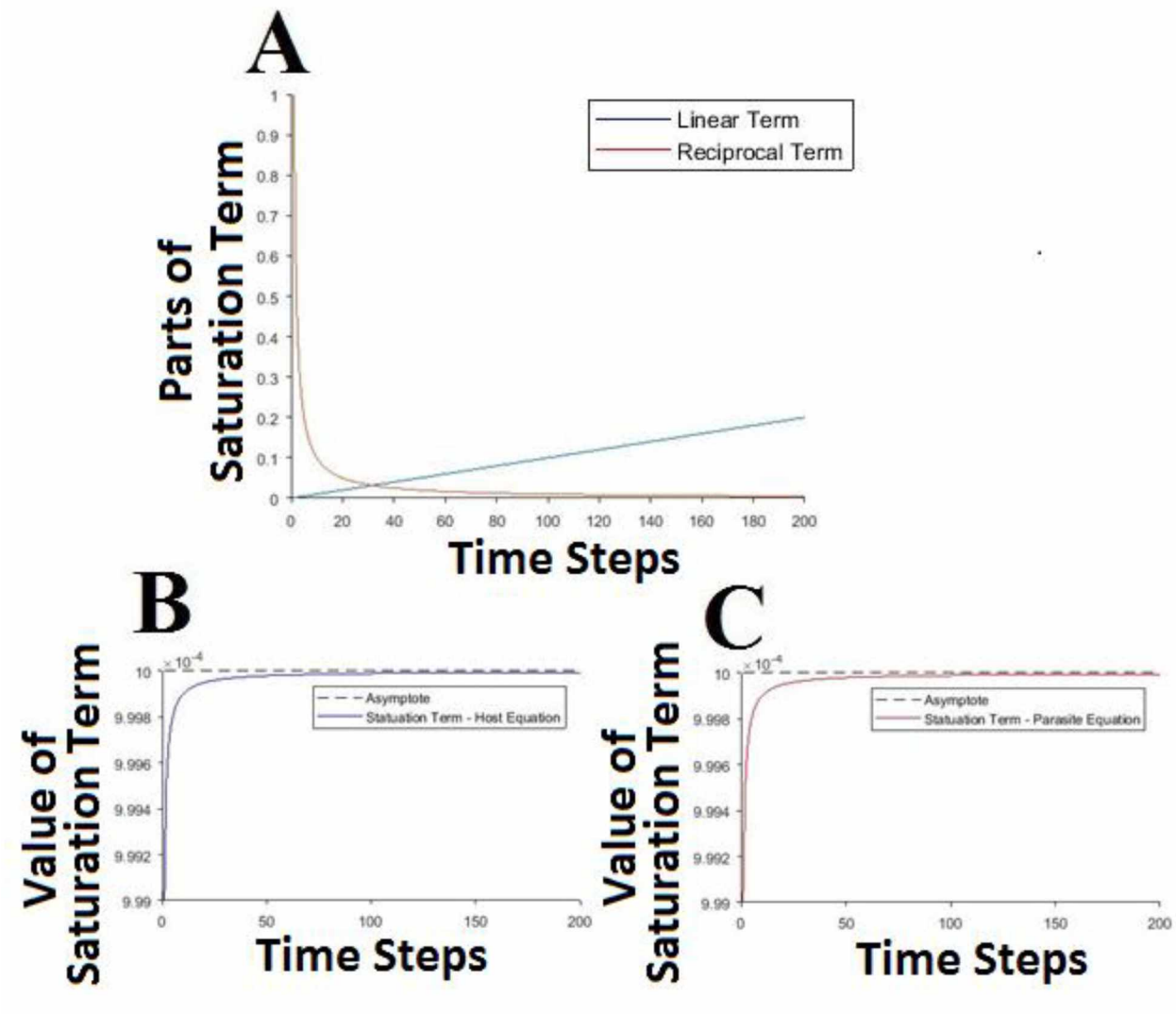

Figure 12: Construction of the saturation term in the saturating type II equations. The linear and reciprocal parts of the saturation term plotted on the same graph. It shows that this saturation term results in a horizontal asymptote resulting in the density dependent saturating behavior seen in the model.

can be seen when the term is broken up into a reciprocal function term multiplied by a linear term with P=1 and c=1 for simplicity. The results of equation (9) are plotted in Figure 12A to show how the saturating behavior is generated in this model.

In the reciprocal function, the parameter a is the vertical asymptote and must fall in the second quadrant to have physical meaning because an infinite population density is impossible. This means that a must have a positive value. For large values of H, this reciprocal function approaches zero, meaning that the product of it with the linear H term approaches zero. This means that the combined term approaches a horizontal asymptote shown in the bottom two plots in Figure 12C, D. This occurs at c. Once at c the host death rate (or parasite birth rate) stays constant at the value of c. Finally that last term in equation (7) is the linear death rate, d, of parasites.

The limit cycle only exits at certain parameter values (Otto & Day, 2007). To find these we need to find the fixed points of the saturating type II equations. We then find where the stability of those fixed points changes from stable to unstable (Strogatz, 2015). Once in a parameter region where an unstable fixed point exists, we plot the phase space to search for a limit cycle around the fixed point (Strogatz, 2015). To find the fixed points we start by setting both equations to zero,

$$0 = \gamma H\left(1-\frac{H}{k}\right) - \frac{cHP}{a+H}, \tag{10}$$

$$0 = \frac{bcHP}{a+H} - dP\ , \tag{11}$$

and solving for the equilibrium values, H^* and P^*.

There are three sets of equilibrium values for H^* and P^*. These are the fixed points:

$$(H_1^*, P_1^*) = (0,0), \tag{12}$$

$$(H_2^*, P_2^*) = (k,0), \tag{13}$$

$$(H_3^*, P_3^*) = \left(\frac{ab}{bc-d}, \gamma\left(\frac{ad}{k(bc-d)}\right)\left(\frac{ab}{bc-d}\right)\right), \tag{14}$$

We then calculate the Jacobian,

$$Jacobian = \begin{pmatrix} \gamma - \frac{2\gamma H_i^*}{k} - \frac{cP_i^*}{a+H_i^*} + \frac{cH_i^* P_i^*}{(a+H_i^*)^2} & -\frac{cH_i^*}{a+H_i^*} \\ \frac{abcP_i^* + 2bcH_i^* P_i^*}{(a+H_i^*)^2} & \frac{bcH_i^*}{a+H_i^*} - d \end{pmatrix}, \quad (15)$$

for the saturating type II equations given in equation (15).

The Jacobian is then evaluated at each of the three fixed points (Blanchard et al., 2006). For each of these three matrixes we find the eigenvalues. By comparing the values of the eigenvalues to the trace determinate plane, we find the stability of the fixed points. If both real parts of the eigenvalues are negative, the fixed point is stable and no stable limit cycle is possible around the point. If one eigenvalue is positive and the other is negative then the point is a saddle and unstable with no limit cycle possible around the point. If both real parts of the eigenvalues are positive, the fixed point is unstable. This does not guarantee a stable limit cycle, but does give a place to look for a stable limit cycle. Since this equation is well known to have a stable limit cycle, I used MATLAB to find eigenvalues with real positive components and then looked at the phase space plots to find the limit cycle. In plotting ten initial conditions taken from the Latin hyper cube sampler, all initial conditions marked as red stars time evolve toward the limit cycle, see Figure 13. This limit cycle can be seen as the prominent loop on the phase space graph. Any initial condition that finds its way onto the loop stays there for all time.

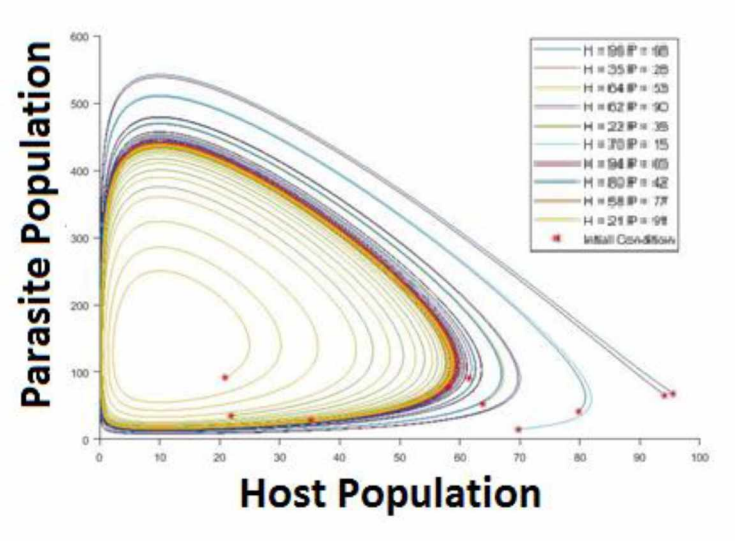

Figure 13: Initial condition attracted to the saturating type II limit cycle. The ten initial conditions are plotted as the red star. As the system time evolves, these simulations all end up on the limit cycle.

The parameters I found that produced this limit cycle were k = 100, a=50, b=6, c=4, d=4, and γ=10. The fixed points occurred at (0,0), (100,0), and (15, 135). The eigenvalues for these three were -4 and 10, -10 and 12, and 1.0740+5109i and 1.0740-5109i. This implies the first two fixed points are saddles so cannot have a limit cycle. The final fixed point is unstable and by looking at the phase space has a stable limit cycle (Strogatz, 2015). This is the limit cycle that I chose to use in my model.

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